REVISION OF THE ORDOVICIAN CARPOID FAMILY IOWACYSTIDAE

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ABSTRACT. Newly discovered specimens and re-evaluation of previous evidence indicate a much closer relation between the solutan carpoids *Belemnocystites*, *Myeinocystites*, *Scalenocystites*, and *Iowacystis* than was previously suspected. Comparative studies of all known species, including observations on the ontogeny of *S. strimplei* Kolata and *I. sagittaria* Thomas and Ladd, show that numerous thecal and steleal structures are homologous. In light of the obvious affinity shown by these carpoids, it is proposed that the Family Belemnocystitidae (*Belemnocystites*, *Myeinocystites*, and *Scalenocystites*) be synonymized with the Family Iowacystidae (*Iowacystis*). The likely synonymy of *Belemnocystites* and *Myeinocystites* is suggested from a re-examination of the holotype of *B. wetherbyi* Miller and Gurley. All species are redescribed and illustrated. A new species, *M. crossmani*, is described from the Trentonian (Caradocian) Dunleith Formation (Galena Group) of Illinois and Iowa. The dorso-ventrally depressed theca, high degree of bilateral symmetry, anterior mouth, and flexible, caudal appendage suggest that the iowacystids were vagrant bottom-dwelling echinoderms that were adapted to a browsing mode of life. They very likely lived with the oral opening and ambulacral groove facing the substrate. The iowacystids inhabited warm, shallow epeiric seas in environments characterized by relatively quiet deposition of carbonate sediments.

CARPOIDS of the Order Soluta (Class Homoiostelea) are rare fossil echinoderms that occur in rocks ranging in age from the Upper Cambrian to the Lower Devonian. They are characterized by a depressed theca that bears a single exothecal arm and a caudal appendage (stele) composed of axially differentiated plates. The body plan is essentially bilaterally symmetrical, with the arm and stele lying at or near the axial plane at opposite ends of the theca.

The iowacystids are a family of solutan carpoids at present known only from the Champlainian and Cincinnatian carbonate facies of North America. They are unique among the Soluta in possessing differentiated thecal plates that have a thick, rigid aboral face, a thin, apparently flexible oral face with a non-marginal arm, and a specialized stele in which the mesistele is undifferentiated from the dististele. The Family Iowacystidae was formerly represented by the single species *Iowacystis sagittaria* Thomas and Ladd. However, study of many new specimens and re-evaluation of previous evidence indicates a much closer relation with three other solutan genera, *Belemnocystites*, *Myeinocystites*, and *Scalenocystites*, than was previously suspected. Comparative studies of all known species show that numerous thecal and steleal structures are homologous. Because of the strong affinity shown by these carpoids it is proposed that the Family Belemnocystitidae, including *Belemnocystites*, *Myeinocystites*, and *Scalenocystites*, be synonymized with the Iowacystidae. In light of the new information, all species are redescribed and illustrated, including one new species of *Myeinocystites*.

TERMINOLOGY

Terminology for symmetry, orientation, and morphology in this investigation in general follows the *Treatise on Invertebrate Paleontology* (Caster 1968, p. S584).

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Problems arise, however, in selecting proper terms for the two thecal surfaces or faces. Caster (1968, p. S583, fig. 372) designated the thecal surfaces according to an inferred habitus, and used obverse, brachial, and carapace as synonyms for the upper surface and reverse, antibrachial, and plastron as synonyms for the lower surface. (Caster employed brachial and antibrachial to refer to the thecal faces whereas Bather 1913, p. 373, originally used the terms to refer to the sides of the theca right or left of the symmetry plane.) Elsewhere Parsley and Caster (1965, p. 114) and Parsley (1972, p. 342) applied the terms 'dorsal' and 'vertral' to the two thecal surfaces in the North American solutan genera. In most solutes, including the Iowacystidae, the habitus suggested above requires the arm to lie on the upper surface away from the substrate, thus suggesting a passive suspension feeding mode of life. Such a mode of life, however, is not substantiated by the flatfish-like body that exhibits a high degree of bilateral symmetry, an anterior (distal) mouth, and a posterior (proximal), flexible, caudal appendage. These morphologic features strongly suggest a vagile browsing existence (Kolata 1973, p. 973).

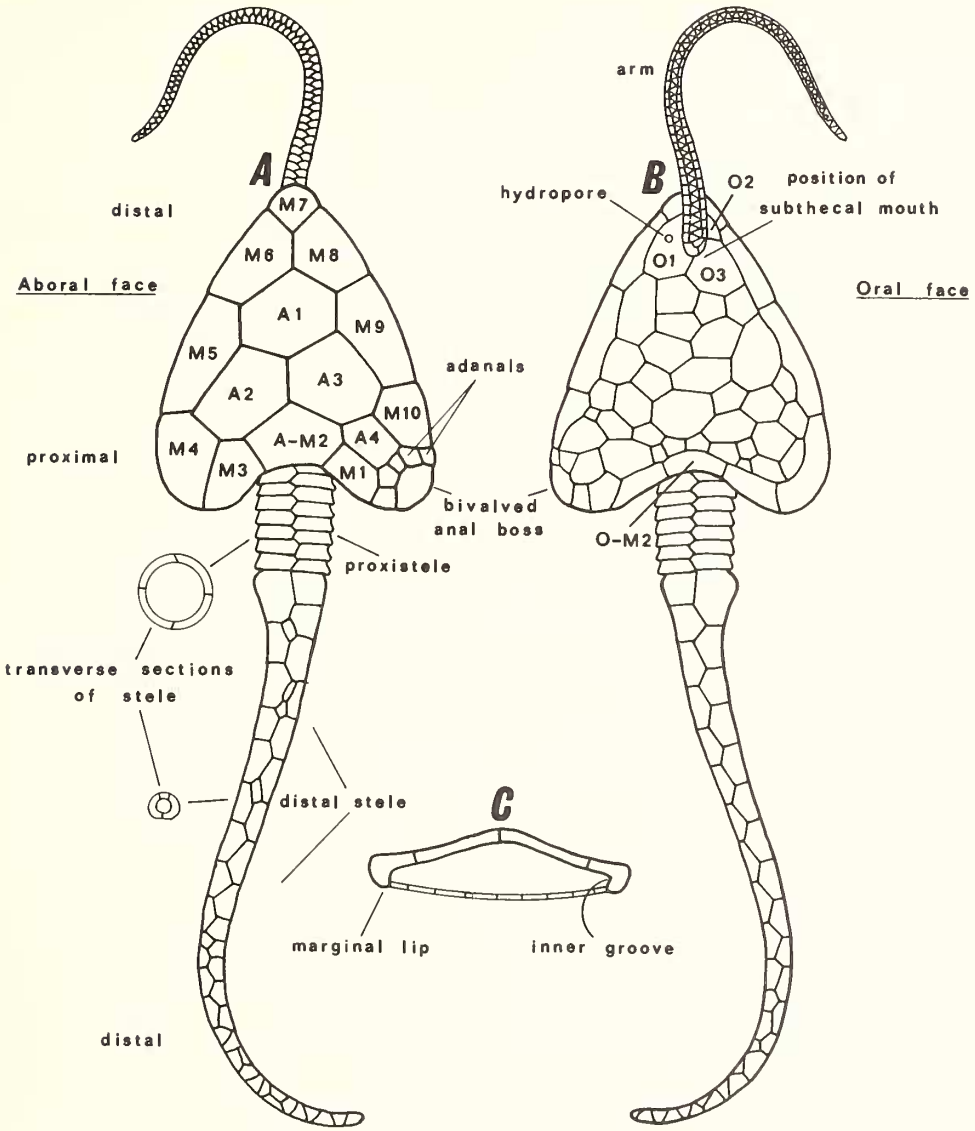
Inasmuch as the true habitus is unknown, we prefer to use the strictly descriptive terms oral and aboral to refer to the two thecal faces. The oral thecal face is that surface on which the mouth is located. It is also the thecal face on which the ambulacral groove, at the base of the arm, is exposed when the cover plates are open. In the iowacystids it is the surface from which the arm emerges. The aboral face is opposite the oral face.

To show the homologous features within the Belemnocystitidae, Parsley (1972, p. 342) proposed a system of nomenclature for thecal plates that is similar in part to that used for the stylophoran mitrate carpoids (Ubaghs 1968, p. S499) and is in part a modification of the system used by Thomas and Ladd (1926) for *Iowacystis*. The nomenclature is very useful in comparative studies of solutan carpoids. Some changes, however, are needed to describe the significant morphologic features in the simplest, clearest manner. First, as mentioned above, the designation of dorsal and ventral thecal plates (D1, D2, V1, V2, and so on) should be avoided. The more objective terms aboral and oral should be substituted (A1, A2, O1, O2, and so on). Secondly, nomenclature for the marginals is so similar to that used for the mitrate carpoids that there is some risk in confusing homoeomorphy for homology. In addition, Parsley's (1972, p. 343, text-fig. 1) marginal M1 is based solely on Wetherby's (1881) questionable drawing of an anomalous solute that is very much different from known solutan carpoids. A more desirable plan would be to designate the marginal plates M1, M2, M3, and so on, beginning with the right lateral adsteleal plate (aboral face up) and counting clockwise to the first anal plate (text-fig. 1).

For descriptive purposes the carpoids discussed herein are oriented with the arm at the anterior end and pointing upwards on the page. Caster's (1968, p. S583) restrictions on the terms 'right' and 'left' are not followed in this discussion.

MORPHOLOGY

The iowacystids possess differentiated thecal surfaces, one side (aboral) of which consists of thick, regular plates that form a rigid frame to the theca. The base of the arm is relatively far from the margin of the theca and is surrounded by three or four



TEXT-FIG. 1. Iowacystid morphology and terminology based on *Iowacystis sagittaria* Thomas and Ladd, 1926. A, aboral face, and B, oral face, showing revised thecal plate nomenclature. C, transverse section of the theca showing the relatively thick aboral plates (upper surface) and nature of contact with thinner, more numerous oral plates (lower surface). Approx. × 1·5.

distinct plates, one of which has a poriferous cone-shaped structure generally interpreted as the hydropore. The stele differs from that of most solutan carpoids in having only two parts instead of three, the dististele being undifferentiated from the mesistele.

Theca. Like other solutan carpoids, the iowacystids have a depressed theca consisting of a mosaic of plates. Thecal outlines vary from irregularly oval to trigonal, depending in part on the stage of ontogeny. In cross-section the oral face is planate to slightly convex and the aboral side is convex. The position of the stele and arm along the longitudinal axis at opposite ends of the theca imparts a high degree of bilateral symmetry, but the oral-anal axis does not correspond with the axial plane as it does in most animals possessing primary bilateral symmetry. Thecal plate patterns, also, are not bilateral.

The aboral face consists of thick, tightly sutured plates that form a rigid carapace to the theca. The plates of the iowacystids are arranged in a characteristic pattern and are readily homologized. The marginal series typically consists of eleven regular plates, including the adsteleal plate (O-M2) of the oral face and excluding the anal series (text-fig. 1). Enclosed within the marginal series are regular somatic plates, typically four in number: the A1 in an anterior position, A2 and A3 centrally located with the suture between them lying on or near the axial plane, and A4 located between A3 and the anal plates. Variations occur in the aboral thecal plates, but homologies can easily be inferred from size, shape, and position in relation to surrounding plates.

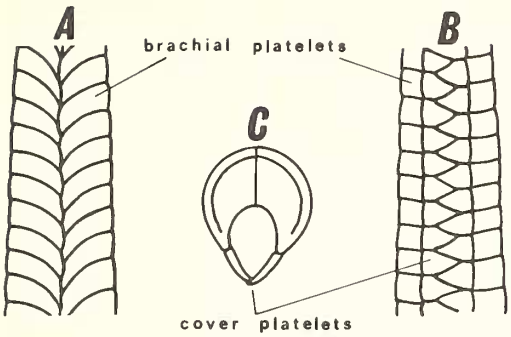
The adsteleal plates are noteworthy in that they form the frame around the stele. Four marginal plates, including the M1, A-M2, O-M2, and M3, form a rigid girdle with a circular to slightly eliptical (in extensiplane) foramen. A marginal flange encircles the foramen and extends out over the first proxistele tetramere. The first tetramere was probably attached by connecting tissue to the recessed surface inside the marginal flange.

The oral face of the theca bears the hydropore, arm, and subthecal mouth. Plating is mosaic, with firm sutures between the anterior plates, particularly the adbrachials; the other plates are relatively thin and apparently had integumentary junctures that provided some flexibility to the oral face. The hydropore is invariably located immediately left (oral face up) of the arm, on adbrachial plate O1. It consists of one or more pores at the top of a cone-shaped tubercle. The subthecal mouth is located at the base of the arm, within a small vestibule formed by the adbrachial plates.

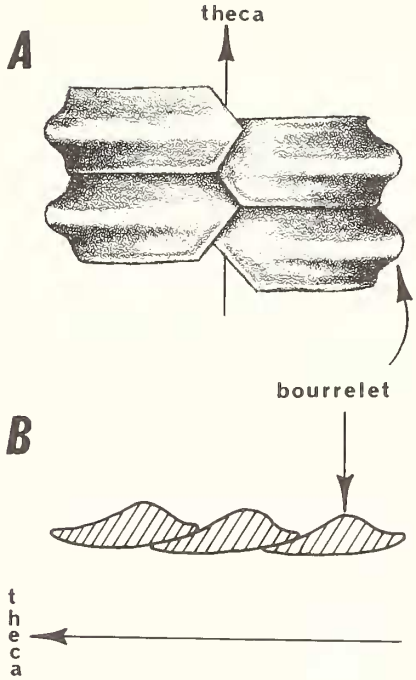
The anus is located in the left (oral face up) proximal corner along the thecal margin, between marginals M1 and M10. Its presence is marked by two quarter-sphere plates that opened along the extensiplane. Additional small, quadrangular adanal plates encircle the valvate quarter-spheres in *Iowacystis* and *Scalenocystites.*

Arm. The single arm is a tapering, unbranched appendage consisting of biserial brachial platelets that curve around the ambulacral groove and smaller biserial platelets that serve as cover platelets (text-fig. 2). Arm length varies from one individual to another but commonly is as long or slightly longer than the theca. Although the arm bears a striking resemblance to some cystoid brachioles, it differs fundamentally in that it is an extension of the body cavity rather than a solid serial skeleton. Whereas cystoid brachioles are mounted on plates outside of the thecal wall, the solutan arm is supported by plates that surround a foramen that opens directly into the body cavity.

The exothecal nature of the arm suggests that the nervous, hemal, and water-vascular systems may have extended into the distal portions as they do in the arm of



TEXT-FIG. 2. Morphology of iowacystid arm based on *Scalenocystites strimplei* Kolata, 1973. A, B, aboral and oral views of arm, respectively, showing brachial platelets and cover platelets. C, cross-section of arm. Approx. ×8.



TEXT-FIG. 3. Proxistele morphology, based on *Scalenocystites strimplei* Kolata, 1973, A, aboral view. B, diagrammatic longitudinal section of three imbricated, partial tetramere rings. Approx. ×10.

a crinoid. A single radial water-vascular canal probably rested within the ambulacral groove. The cover platelets very likely could be opened to allow protraction of tube-feet (Nichols 1972, p. 530).

Stele. Unlike most solutan carpoids that possess a tripartite stele differentiated into a proxistele, a mesistele, and a dististele, the iowacystids (not confirmed in *Belemnocystites*) are characterized by a two-part structure consisting of a proxistele with telescopically imbricated tetramere rings and an undivided distal stele. Plate organization typical of a mesistele persists through all of the distal stele. (In order to avoid the homologous inferences of the terms 'dististele' and 'mesistele' in the following discussion, the less-restricted term 'distal stele' will be used to refer to all of the stele that is distal to the proxistele.)

The proxistele is round to slightly elliptical in tranverse section and consists of from five to ten tetramere rings that enclose a large central lumen. Each tetramere consists of a thickened ring (bourrelet) with a thin rim that imbricates within the proximally adjacent ring (text-fig. 3). The rim of the first tetramere fits snugly into the recessed edge of the foramen formed by the adsteleals.

The juncture between the proxistele and distal stele is abrupt. The distal stele is essentially a biseries of thick polygonal plates that enclose a small central lumen that extends to the distal tip of the stele. The biseries is most evident on the oral side but is interrupted along the medial portion of the aboral side by small intercalate plates that increase in number towards the distal tip.

PHYLOGENY

Morphologic traits possessed by the ancestral iowacystid stock can be inferred by comparing the four known genera. The presence of well-differentiated thecal faces in these genera, for example, strongly suggests that this morphologic character was present in the ancestor. In addition, a high degree of regularity in the aboral somatic and marginal plates was most likely well established. Regularity of the adbrachial plates would also be expected. The remaining oral face plates, however, were probably relatively numerous and irregular in size and shape. The characteristic distal stele with mesistele undifferentiated from the dististele is also considered to have been present in the ancestor.

Perhaps *Scalenocystites* (Trentonian Stage of Middle Ordovician), with its asymmetric theca and numerous irregular oral somatic plates is most like the iowacystid ancestor. Although *Myeinocystites* (Blackriveran Stage of Middle Ordovician) is known from slightly older strata, the relatively few, regular plates on its oral face seem to be of a specialized character. *Scalenocystites* is judged to be of, or close to, the lineage that led to *Iowacystis* (Cincinnatian Stage of Upper Ordovician). Both genera have similar thecal outlines, oral face organization, and marginal ornament. *Iowacystis* is more advanced than *Scalenocystites*, possessing a higher degree of bilateral symmetry, a more complex system of nodes, cusps, and ridges on the marginals, and fewer axial intercalates at the juncture between the proxistele and distal stele.

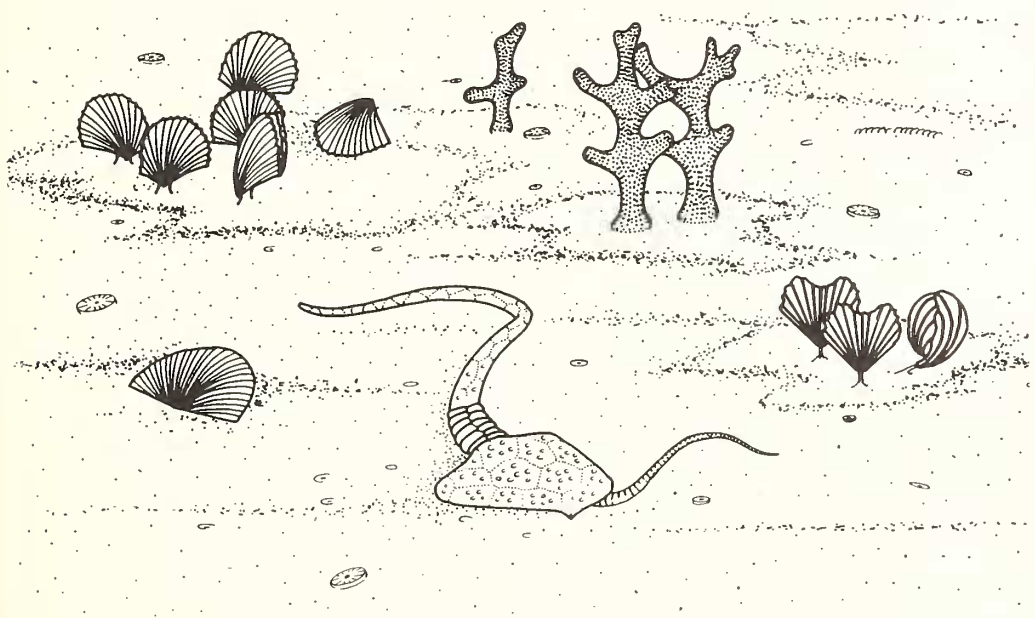
PALAEOECOLOGY

The iowacystid carpoids occur in argillaceous limestone and dolostone that consist of whole and broken, unabraded, occasionally articulated, shelly invertebrates 'floating' in a fine-grained matrix. The rocks, for the most part, lack any evidence of strong currents and appear to have been formed in environments that were relatively far from major sources of terrigenous sediment. The iowacystids are typically associated with an abundant and diverse invertebrate fauna consisting largely of brachiopods, bryozoans, molluscs, trilobites, and other echinoderms. The random orientation of shelly debris and the lumpy, irregular beds indicate extensive biogenic activity due to scavengers and burrowers that reworked the sediment prior to lithification. The iowacystids lived in warm, shallow epeiric seas in environments characterized by relatively quiet deposition of carbonate sediments and with *in situ* accumulation of shelly debris.

The morphology of the iowacystids suggests that they were vagrant organisms, probably able to scull across the sea bottom by means of the caudal appendage (Parsley 1972, p. 347; Kolata 1973, p. 973). The telescopically imbricated proxistele tetrameres indicate that this part of the stele was quite flexible and capable of movement in all directions. The relatively large proxistele lumen probably contained muscles that facilitated movement of the stele (Caster 1968, p. S594). In contrast to the proxistele, the distal stele was a relatively stiff structure, consisting of thick, closely appressed (tesselate) plates. It does not appear to have had prehensile capability and very likely was not employed as a holdfast. A vagrant mode of life is further

suggested by the depressed, trigonal to oval thecae, bilateral symmetry, anterior mouth, and posterior anus, which is a recurrent body plan in animals that seek out their food. Iowacystid morphology appears to have been well adapted to the hydrodynamic requirements of a bottom-moving flatfish-like existency (text-fig. 4).

The normal living position of the iowacystids was probably with the carapace-like aboral face in the dorsal position and the thinner, flexible, oral surface facing the substrate (Kolata 1973, p. 973). In that position, the thick, pustulose plates of the aboral face would have provided maximum protection for the body. In addition, the arm, with its food groove facing the substrate, could have been used to browse on the accumulation of organic debris on the substrate rather than to wait passively for food-bearing currents to bring nutrients to the animal. A similar orientation and mode of life has been suggested for homoeomorphs of the Iowacystidae, such as the cystoids *Amecystis* (Broadhead and Strimple 1975) and *Pleurocystites* (Paul 1967).



TEXT-FIG. 4. Reconstruction of Middle Ordovician sea floor showing inferred life mode of *Scalenocystites strimplei* Kolata, 1973.

Although the iowacystid carpoids are very rare fossils, they are sometimes found in clusters on bedding planes, suggesting a gregarious habit during life. This has been noted in the occurrence of *Scalenocystites* from the Dunleith Formation (Galena Group) of Minnesota and *Iowacystis* (Pl. 63, fig. 1) from the Fort Atkinson and Scales Formations (Maquoketa Group) of Iowa. Specimens of *Myeinocystites crossmani* n. sp. from the Dunleith Formation near Rockton, Illinois, were found in an unusually diverse cluster of echinoderms that included cystoids (*Pleurocystites*), crinoids (*Carabocrinus*, *Cupulocrinus*, and *Glyptocrinus*), edrioasteroids (*Edrioaster*),

cyclocystoids (*Cyclocystoides*), and echinoids (*Neobothriocidaris*) (Kolata 1975). The cluster occurred on a single bedding plane in an area of approximately 2 sq. ms. *M. crossmani* n. sp. was found with a similarly diverse cluster of echinoderms in the Dunleith Formation near Burr Oak, Iowa.

SYSTEMATIC DESCRIPTIONS AND DISCUSSION

Phylum ECHINODERMATA Fleming, 1828
Subphylum HOMALOZOA Whitehouse, 1941
Class HOMOIOSTELEA Gill and Caster, 1960
Order SOLUTA Jaekel, 1901
Family IOWACYSTIDAE Gill and Caster, 1960
(Belemnocystitidae Parsley, *in* Caster 1968; in part)

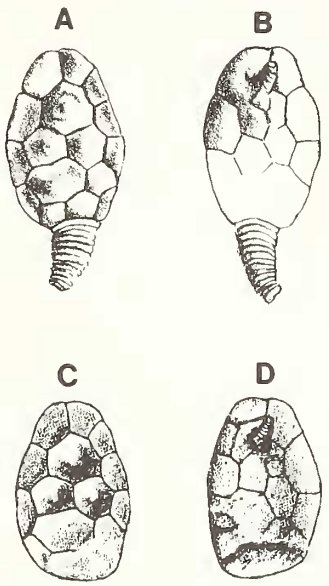
Genera. Iowacystis Thomas and Ladd, 1926; *Belemnocystites* Miller and Gurley, 1894; *Myeinocystites* Strimple, 1953; *Scalenocystites* Kolata, 1973.

Emended diagnosis. Oval or trigonal, depressed theca with differentiated thecal faces; basically asymmetric theca with well-developed bilateral symmetry. Aboral face composed of relatively few, thick, tightly sutured plates with large marginals that envelope edges forming a rigid frame to the theca; convex near centre, concave near edges; aboral plates readily homologized within the family. Oral face composed of a mosaic of thin thecal plates of varied size, shape, and number; integumentary junctures near the centre of the face. Oral face bears single exothecal arm consisting of two matching but unequal biseries of platelets; base of arm located proximal to anterior margin and emerges from thecal face; base of arm typically enclosed by three plates, one of which possesses a perforate cone-shaped tubercle generally regarded as the hydropore. Anus located at left (oral face up) proximal margin of theca; closed by bivalved boss. Pustulose ornament on aboral face generally coarser than that on oral face. Four firmly sutured adsteleal plates form a rigid girdle around the stele. Stele round to slightly depressed; proxistele consists of five to ten telescopically imbricated tetramere rings; axial intercalates on aboral side of distal stele; mesistele undifferentiated from dististele.

Remarks. Thomas and Ladd (1926) described *I. sagittaria* from the Cincinnatian (Upper Ordovician) Maquoketa Group of north-eastern Iowa and provisionally assigned it to the stylophoran Anomalocystitidae, adding, 'The genus may eventually be relegated to a new family'. Bather (1926, pp. 233–234; 1928, pp. 5–7), however, rejected Thomas and Ladd's classification and properly noted its solutan affinities, stating (1926, p. 234), '. . . that it is a *Dendrocystis* [*sic*] at about the same level of evolution as *D. scotia* though on different lines'. Although some attempt was subsequently made to resurrect the name *Iowacystis* (Dehm 1934, p. 21), it was considered to be a synonym of *Dendrocystites* by most authors until Gill and Caster (1960, pp. 20–22) redefined the genus and proposed the Family Iowacystidae to receive the single species. Gill and Caster (1960, p. 21) considered the depressed theca with differentiated 'anal and antianal surfaces', trigonal outline, and arm attachment on the thecal face rather than on the distal margin to be specialized features that clearly

marked the family off from other solutan carpoids. When the type specimens of *I. sagittaria* were re-examined by Parsley and Caster (1965), several details were added to the specific description. Additional discussion of the comparative morphology was given by Caster (1968).

Wetherby (1881, p. 177) briefly described and illustrated with drawings an apparent solute from Trentonian (Middle Ordovician) rocks of Kentucky. He designated the single specimen, 'Cystidean, New Genus and Species', but hesitated to carry the taxonomy further because of the lack of study material. His two drawings (oral and aboral views of the theca) show an oval-shaped theca approximately 22 mm in length that has a small arm on the oral face and a portion of an apparent 'proxistele' attached to one end. The pattern of thecal plates on the aboral face bears a strong resemblance to iowacystid genera, except for an anomalous thecal plate that is shown at the juncture with the stele. Furthermore, the 'proxistele' is shown to taper abruptly (fifteen holomerous segments) to one-half its diameter at a distance of 10 mm from the juncture with the theca. This is unusual because in well-preserved solutes the proxistele invariably consists of tetrameres that taper very little distally. Recent attempts to locate the Wetherby specimen have been unsuccessful, and it has been generally assumed by many investigators to be lost.



TEXT-FIG. 5. Photographs of A, aboral face, and B, oral face of a specimen, illustrated by Wetherby (1881, pl. 5, fig. 2, 2*a*) and named 'New Genus and Species'. C–D, *Belemnocystites wetherbyi* Miller and Gurley, 1894, photographs of aboral and oral faces of the holotype (FMNH UC 6046) illustrated by Miller and Gurley (1894, pl. 1, figs. 5 and 6). ×1.

Miller and Gurley (1894, p. 9) described and illustrated a single specimen from Trentonian rocks of Kentucky and assigned it to a new genus and species, *Belemnocystites wetherbyi* (specific appelation in honour of A. G. Wetherby), referring it to the stylophoran family Anomalocystitidae. The specimen (holotype FMNH UC 6046; Field Museum of Natural History, University of Chicago) is remarkably similar in size and shape to the specimen described by Wetherby (1881) (text-fig. 5). In fact, when the two drawings are superimposed, the outlines correspond almost exactly, except that the Miller and Gurley specimen lacks the extra adsteleal plate and terete, holomerous proxistele that make the Wetherby specimen so anomalous. In the generic description Miller and Gurley (1894, p. 9) stated, 'Column comparatively large composed of thin plates and tapering as in *Steleocystites*', but they do not illustrate the column. This suggests that they either studied an isolated fragment or relied on the Wetherby drawings for information. The unusual adsteleal plate and 'proxistele' shown by Wetherby may have been an isolated fragment (possibly the proximal stem and thecal plate of a glyptocystitid cystoid) that was assumed to be part of the solutan theca. Miller and Gurley did not mention who collected the specimen or how it was obtained, and it seems likely that they merely redescribed Wetherby's specimen and assigned

a name to it. If this is so then the Wetherby specimen is in fact the holotype (FMNH UC 6046) of *B. wetherbyi*.

Parsley (*in* Caster 1968, p. S623) recognized the solutan affinities of *Belemnocystites* and referred it to the new Family Belemnocystitidae of the Order Soluta. Unfortunately, the paucity of study material forced Parsley to rely heavily on Wetherby's (1881, pl. 5, figs. 2, 21) drawings in order to define the taxobasis of the new family. The extra adsteleal plate and unusual holomerous stele were regarded as valid features of this monotypic family. Parsley (*in* Caster 1968, p. S623) also recognized that *Belemnocystites* bears several traits in common with *Iowacystis*, including 'configuration, location and interrelationship of the arm and pore plate, unusual somatic biconvexity of the theca, and similar nature and symmetry of the ventral somatic plates, including what appears to be an azygous adanal plate'.

Later, in a paper concerning the homeomorphy between the solutan Belemnocystitidae and the stylophoran Anomalocystitidae, Parsley (1972, p. 341) assigned *Myeinocystites natus* Strimple (1953) from the Middle Ordovician of Oklahoma and Tennessee to the Belemnocystitidae. (Strimple 1953, p. 105, had previously assigned *M. natus* to the stylophoran Anomalocystitidae.) Parsley (1972, text-fig. 1C–E) again referred to the Wetherby drawing to show the presumed nature of the theca and stele in *Belemnocystites*. In addition, a topotype of *B. wetherbyi* was illustrated (Parsley 1972, pl. 1, figs. 3, 5–6). This specimen (USNM 14201), although silicified, is a complete theca that shows the thecal plate pattern (ibid., pl. 1, fig. 6) and the nature of the adsteleal plates (ibid., pl. 1, fig. 3). The theca is similar to *Myeinocystites*, *Scalenocystites*, and *Iowacystis* and does not possess the extra adsteleal plate illustrated by Wetherby.

It is evident from re-examination of old material and the discovery of many new specimens that the Family Belemnocystitidae, including the genera *Belemnocystites*, *Myeinocystites*, and *Scalenocystites*, shares a great many morphologic features with *Iowacystis* (Iowacystidae). Furthermore, the diagnosis of the Family Belemnocystitidae (Parsley, *in* Caster 1968, p. S623; Parsley 1972, p. 342) is not sufficiently distinct from that of the Iowacystidae (Gill and Caster 1960, p. 20; Caster 1968, p. S620) to require two family-level taxa. In his original diagnosis Parsley (*in* Caster 1968, p. S623) stated that the Belemnocystitidae were 'Solutes with regularized marginal and somatic plates; single, nonterminal, biserial arm with adjacent coniform pore plate. Stele holomerous [the tetramerous nature of the proxistele was later recognized by Parsley 1972, p. 342 in a revised family diagnosis] or apparently so. Characters essentially those of type genus.' Except for the differences in thecal outline, these characteristics apply equally well to the Family Iowacystidae and, in part, are the basis for differentiating *Belemnocystites*, *Myeinocystites*, *Scalenocystites*, and *Iowacystis* from all other known solutan carpoids. The differences in thecal outline are judged to be important at the generic level but are outweighed on the family level by the obvious homologous thecal and steleal structures that characterize the four genera. It is proposed here that the Family Belemnocystitidae be included in with the Iowacystidae.

Genus IOWACYSTIS Thomas and Ladd, 1926

Type species. Iowacystis sagittaria Thomas and Ladd, 1926, p. 6.

Diagnosis. Isosceles-triangle-shaped thecal outline; thecal faces differentiated; marginal plates possess a thickened rim with prominent arcuate ridges and grooves, particularly on lateral edges; marginal M7 not in contact with somatic A1 unless the latter is compound; oral face plates numerous (about forty) and irregular; base of arm and subthecal mouth enclosed by three regular adbrachial plates; bivalved anal boss surrounded by small quadrangular adanal plates on both faces; distal stele typically consists of three plates at juncture with proxistele.

Iowacystis sagittaria Thomas and Ladd, 1926

Plate 62, figs. 1–12; Plate 63, figs. 1–5; Plate 64, fig. 10; text-figs. 1, 6, 7, 8A

1926 *Iowacystis sagittaria* Thomas and Ladd, p. 6, pl. 1, figs. 1–5; pl. 2, fig. 1; pl. 4, figs. 1–6; pl. 5, figs. 1–2.
1926 *Dendrocystis sagittaria* (Thomas and Ladd) Bather, pp. 233–234.
1928 *Dendrocystis sagittaria* (Thomas and Ladd) Bather, pp. 5–7.
1933 *Jowacystis* [sic] *sagittaria* Thomas and Ladd, Dehm, p. 65.
1934 *Dendrocystites* (*Iowacystis*) *sagitarus* (Thomas and Ladd), Dehm, p. 37.
1938 *Dendrocystites sagittaria* (Thomas and Ladd) Bassler, pp. 9, 85.
1941 *Dendrocystis sagittaria* (Thomas and Ladd) Chauvel, pp. 7, 241.
1943 *Dendrocystites sagittarius* (Thomas and Ladd) Regnéll, pp. 41, 195.
1960 *Iowacystis sagittaria* Thomas and Ladd, Gill and Caster, pp. 20–22, 24, 29.
1965 *Iowacystis sagittaria* Thomas and Ladd, Parsley and Caster, pp. 141–153, pl. 17, figs. 1–8; pl. 18, figs. 1–7.
1968 *Iowacystis sagittaria* Thomas and Ladd, Caster, p. S620.

Type specimens. Thomas and Ladd (1926) designated seven syntypes for *I. sagittaria*, including SUI 3525–3528; three stele fragments were catalogued as syntypes SUI 3529-A, -B, and -C. All specimens are in the repository of the Department of Geology, University of Iowa, Iowa City, Iowa.

Material. In addition to the syntypes, thirty-three newly discovered specimens also were studied; eighteen are reposited at Iowa City, including SUI 39433–39450.

Age. Cincinnatian Series (Upper Ordovician–Caradocian–Ashgillian).

Localities. The type specimens are from the Fort Atkinson Formation (bed no. 9 of Parker *et al.* 1959) of the Maquoketa Group (stratigraphic classification in the Upper Mississippi Valley region after Templeton and Willman 1963) at Fort Atkinson, Winneshiek County, Iowa. In addition, specimens are known from beds 7, 8, and 9 (lower part of Fort Atkinson Formation) of Parker *et al.* (1959) in a roadcut on the south edge of Fort Atkinson, Winneshiek County, Iowa, at the north centre line, Sec. 10, 96N.–9W., Decorah Quadrangle, and from the same unit 0·5 km south of Elgin, Fayette County, Iowa, SW. corner Sec. 24, 94N.–7W. *I. sagittaria* is also known from the greyish brown, argillaceous, dolomitic limestone of the *Vogdesia* Zone, Elgin Member, Scales Formation, Maquoketa Group at the following localities: roadcut on north side of Winneshiek County Highway B-32, 3·7 km east of Fort Atkinson, Winneshiek County, Iowa, SW. NE. Sec. 15, 96N.–9W., Decorah Quadrangle; quarry located 5·6 km south-east of Ossian, Winneshiek County, Iowa, NE. SW. Sec. 33, 96N.–8W., Decorah Quadrangle; roadcut on west and south sides of curve in road, 8·0 km south of Ossian in Fayette County, Iowa, SW. Sec. 2, 95N.–8W., Decorah Quadrangle; quarry located 9·6 km north of Cresco, Howard County, Iowa, NW. NW. Sec. 24, 100N.–11W., Mason City Quadrangle; roadcut on south side of road, 4·0 km east of Eldorado, Fayette County, Iowa, NE. NE. Sec. 9, 95N.–8W., Decorah Quadrangle.

Diagnosis. Same characteristics as genus.

Description of adults: Theca. The depressed, sagittiform theca is biconvex in cross-section and possesses differentiated thecal faces. The arm emerges from the oral face near the apex or distal tip of the theca. The arm and stele lie near the principal plane of symmetry accentuating the well-developed bilateral symmetry.

The aboral face consists of thick (0·5–0·6 mm) plates that are generally uniform in size, shape, and position. The marginal series typically consists of ten plates (excluding marginal O-M2 and the anal plates) that form a rigid frame for the theca. The marginal plates form the thecal edges and extend around to the oral face, where they occupy a narrow peripheral band. The marginals are thick (up to 4·0 mm thick) at the edges and carry an inner groove (text-fig. 1) that is continuous around the periphery of the theca (visible on oral face). There is a reverse in curvature on the aboral face between the slightly concave marginals and the convex somatic plates.

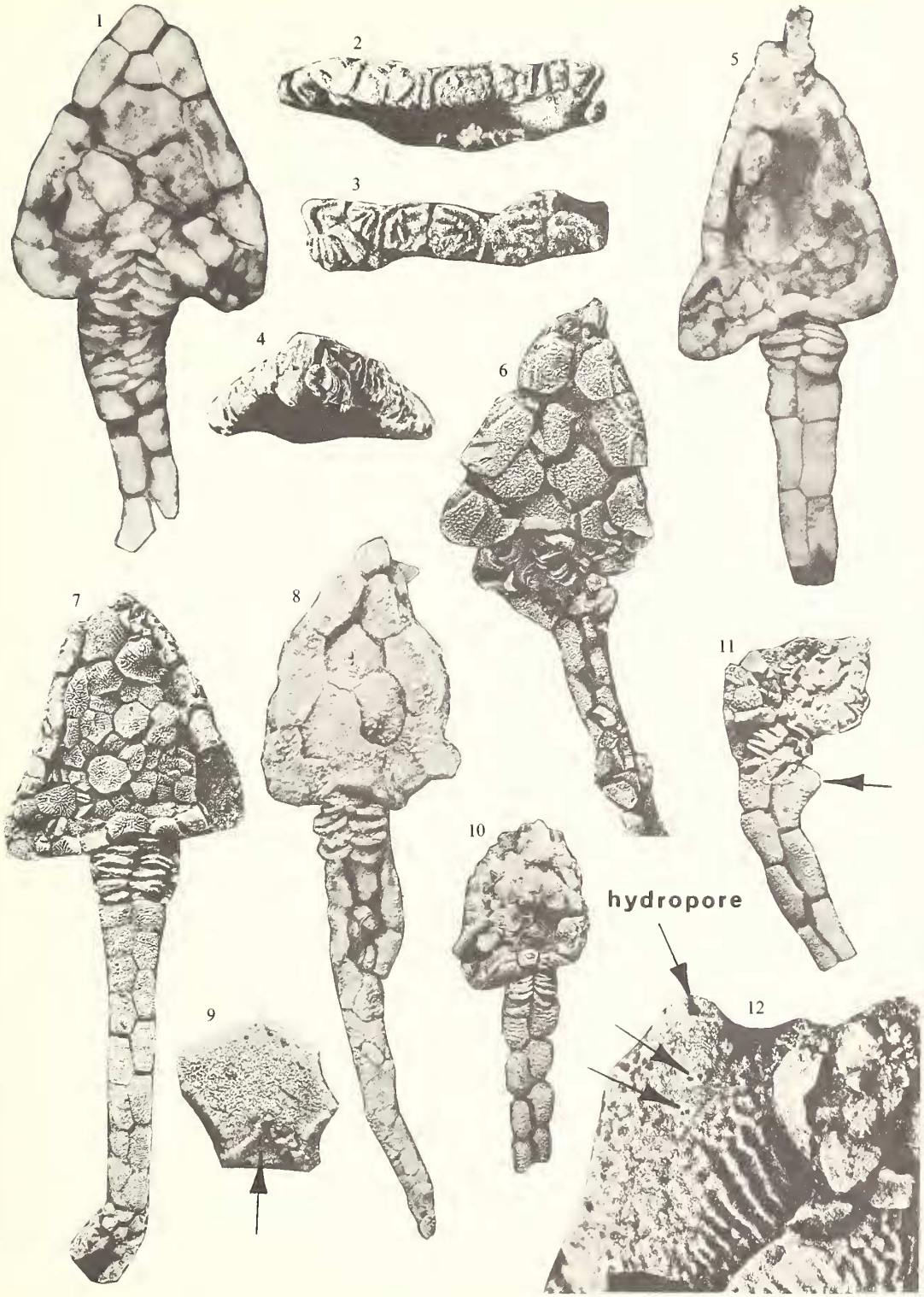
Marginal M4 occupies the left (aboral face up) proximal (posterior) angle of the theca. Marginals M6 and M8 are usually in contact, with the suture between them lying on the plane of symmetry; in some specimens a small somatic plate may lie between the two plates (Pl. 62, fig. 1; text-fig. 6c). Marginal M7 occupies the distal tip of the theca.

Shallow grooves marking the probable sites of muscle attachment are present deep within the foramen along the sides of the M1 and M3 adsteleals (Pl. 64, fig. 10). In addition, a triangular apophysis is sometimes present on the inner proximal edge of the A-M2 adsteleal (Pl. 62, fig. 9). A marginal flange encircles the foramen and extends out over the proximal feather edge of the first proxistele tetramere.

The marginal plates are marked by a series of sharp arcuate ridges that curve around the thecal edges and loop on to the aboral face (Pl. 62, figs. 2–4). One of the most prominent ridges passes from the centre of marginal M4 on the oral face around to the aboral face turns sharply at the juncture of M4 and M5 and curves back around to the centre of M5 on the oral face. The looping pattern is repeated on M5, M6, and M7. A similar pattern occurs along the opposite thecal edge between M7, M8, M9, and M10. Additional nodes, cusps, and secondary ridges occur along the edges

EXPLANATION OF PLATE 62

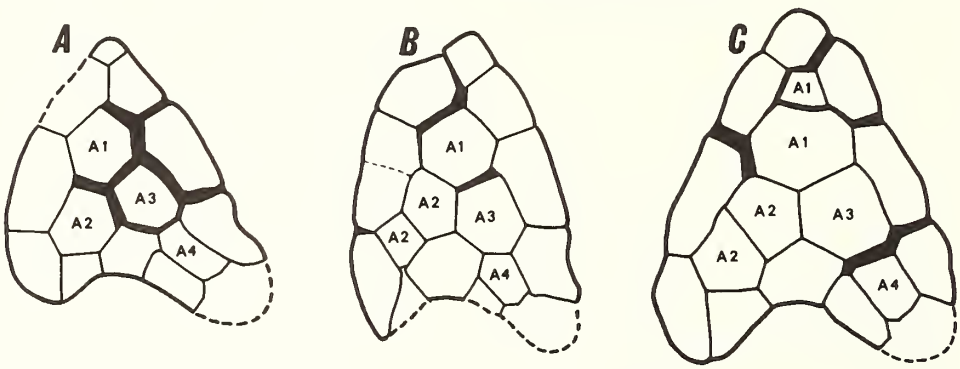
Figs. 1–12. *Iowacystis sagittaria* Thomas and Ladd. 1, aboral face of SUI 39442 photographed under xylol; Elgin Member, Scales Formation (bed no. 4 of Parker *et al.* 1959), Maquoketa Group, near Eldorado, Iowa, ×2·6. 2–4, lateral views of syntype SUI 3526 with aboral face oriented up; 2, right thecal edge showing marginal ornament; position of a possible sutural pore is shown by upper arrow, lower arrow points to hydropore; 3, left thecal edge showing marginal ornament and basal part of the arm; 4, anterior or distal end of theca showing position of the arm and hydropore; Fort Atkinson Formation, Maquoketa Group, Fort Atkinson, Iowa, ×2. 5, oral face of SUI 39434; Elgin Member (bed no. 4 of Parker *et al.* 1959), Fort Atkinson, Iowa, ×4. 6, aboral face of SUI 39437; Fort Atkinson Formation, Elgin, Iowa, ×2. 7, oral face of syntype SUI 3525; same locality as figs. 2–4, ×1·8. 8, aboral face of SUI 39448; same locality as fig. 5, ×4. 9, interior surface of adsteleal marginal A-M2 (SUI 39447); note triangular apophysis along proximal edge at arrow; same locality as fig. 5, ×8. 10, oral face of SUI 39435; same locality as fig. 5, ×3·3. 11, oral face of SUI 39433, note knob-like structure on distal stele at arrow; same locality as fig. 1, ×3. 12, adbrachial plate O1 of syntype SUI 3525 showing hydropore tubercle with hydropore at top and several smaller pores (at lower arrows, accented with ink) below; same locality as figs. 2–4, × 10.



KOLATA *et al.*, *Iowacystis*

within the prominent arcuate ridges. The remainder of the aboral face, including the somatic plates, is covered by numerous small pustules (Pl. 62, fig. 8). A detailed description of the prosopon (ornament) of *Iowacystis* is given by Parsley and Caster (1965, pp. 148–152).

The aboral somatic plates tend to vary in number and shape. Homologous plates or groups of plates, however, are readily apparent. The simplest pattern (Pl. 62, fig. 8; text-fig. 6A) is characterized by four somatics, including the distal A1, central A2 and A3, and right proximal A4, a pattern that is characteristic of *Scalenocystites* and *Belemnocystites*. A common variation of this pattern occurs in specimens (Pl. 63, fig. 2; text-fig. 6B) that possess a compound A2, here interpreted as a homologous pair. The more extreme variants (Pl. 62, fig. 1; text-fig. 6C) possess two homologous pairs, A1 and A2 both being compound. The number of somatics apparently is not related to the size or stage of development. In all specimens observed, the homologous plates and pairs of plates can be determined by their size, shape, and relative position.



TEXT-FIG. 6. *Iowacystis sagittaria* Thomas and Ladd, 1926, showing homologous aboral somatic plates. A, SUI 39441; B, SUI 39439; C, SUI 39442. Approx. ×2·5.

The oral face consists of approximately forty relatively thin (0·2–0·3 mm thick) plates that are mostly irregular in size, shape, and position. The plates are loosely articulated and were apparently held within a flexible integument. The oral thecal plates are sutured to the marginals along the marginal lip (text-fig. 1).

The base of the arm and the subthecal mouth are enclosed by three regular adbrachials, including the O1, O2, and O3 plates (text-fig. 1). These three plates are generally thicker (0·5–0·6 mm) than the more proximal oral somatics. The adbrachials are tightly sutured to each other as well as to marginals M6, M7, and M8. The O1 plate is sutured to M7 and M8 and possesses a prominent cone-shaped tubercle with an apical pore. The axis of the tubercle is oriented at an oblique angle to the upper left (oral face up), with the pore exposed along the thecal margin. Serial sections show that the pore expands into a cone-shaped lumen within the theca. Several smaller pores are sometimes clustered around the main apical pore (Pl. 62, fig. 12); these have been described by Thomas and Ladd (1926, p. 10) and by Parsley and Caster (1965, p. 145). A possible sutural pore was observed along the zigzag suture between the O1 plate and marginal M8 in specimens SUI 39448 and SUI 3526 (Pl. 62, fig. 2).

Surfaces of the oral somatic plates are covered by numerous small pustules many of which have coalesced into fine radiating ridges (Pl. 62, fig. 12). The ridges are particularly well developed on the adbrachials and on the plates in the anal lobe.

The anal opening is covered by a pair of tumid, valvate plates that close along the extensiplane. The bivalve apparatus is surrounded by a number of small, loosely articulated, quadrangular adanal plates. A small vestibule within the anal lobe is outlined by the deeply notched sides (visible on the oral face) of marginals M1 and M10 (Pl. 62, fig. 5). The vestibule is covered on the oral face by a number of small, loosely articulated thecal plates.

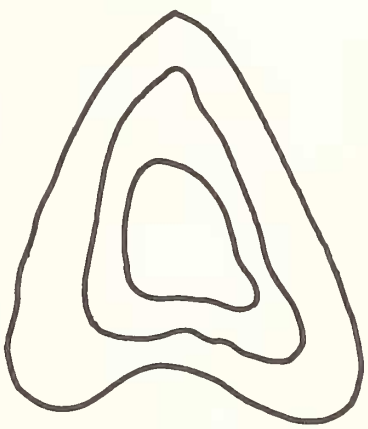
Arm. The arm consists of a large biseries of brachial platelets that carry the ambulacral groove and a smaller biseries of erectile cover platelets (Parsley and Caster 1965, p. 147). Viewed aborally the brachial platelets alternate in a chevron pattern, with the vertices pointing towards the theca. The brachial platelets form the sides of the arm and imbricate along the distal edges. On the oral side, one cover platelet is matched to every brachial platelet on each side of the ambulacral groove.

Stele. The proxistele consists of five to ten telescopically imbricating tetramere rings. A relatively large lumen extends from the inside of the theca to the distal tip of the stele. The distal stele typically consists of three plates at the juncture with the proxistele, thus differing from *Belemnocystites* and *Scalenocystites*, which usually have four plates. In addition, the distal stele is somewhat flat on the oral side and rounded on the aboral side. In a few individuals (Pl. 62, fig. 11) the right (oral face up) distal stele plate at the juncture with the proxistele is expanded into a knob-like structure of unknown function. The mesistele is undifferentiated from the dististele. The distal stele is covered to the tip by numerous small pustules (Pl. 63, fig. 5) similar to those on the oral face of the theca.

Ontogeny. The ontogeny of *I. sagittaria* is based on thirty-seven specimens, nineteen of which possess complete and well-preserved thecae. Thecal lengths (measuring from distal tip of M7 to proximal edge of A-M2) range from 7 to 21 mm, with a generally continuous sequence of sizes represented.

Immature individuals possess an asymmetric thecal outline characterized by a large, protruding anal lobe. The isosceles-triangle-shaped theca of the adults appears to have developed gradually by accelerated growth of the right proximal thecal angle (oral face up) in comparison with the anal lobe (text-fig. 7). In the smaller specimens the right proximal thecal angle is occupied by marginals M3 and M4. In the larger, presumably more mature individuals, however, the thecal angle is occupied entirely by the M4.

The relatively large anal lobe is surrounded by a



TEXT-FIG. 7. Superimposed thecal outlines of three specimens of *Iowacystis sagittaria* Thomas and Ladd, 1926, showing progressive changes through ontogeny; anal lobe is on the lower right. ×3.

number of loosely articulated adanal plates. On the oral face the adanals and oral somatics cover a large vestibule located between the deeply notched sides of marginals M1 and M10. The ratio of the volume of the vestibule to the main part of the theca is appreciably greater in the immature stages than in the adults.

A full complement of aboral thecal plates is clearly developed at the stage of growth represented by the smallest specimens (thecal length 7 mm). As is true for the adults, the aboral somatic plates commonly occur as homologous pairs, particularly the A1 and A2 somatics. The marginals occupy a relatively larger area on the aboral face than the somatics.

In the early ontogenetic stages the aboral face is covered by relatively few, widely spaced pustules. Although size of the pustules is relatively constant throughout development, they tend to increase in number, becoming densely packed in the adults. The characteristic nodes, cusps, and arcuate ridges on the marginals are well developed even on the smallest specimens. (Compare immature, Pl. 62, fig. 8, with adult, Pl. 62, fig. 6.)

Plates on the oral side of the theca in the early growth stages tend to be thin, weakly calcified, and, judging from the wide gaps along the sutures, were apparently quite loosely articulated. Furthermore, there is some suggestion that new plates were added by intercalation during growth. The smaller specimens possess from twenty to twenty-five oral somatics, whereas the adults generally have about forty plates.

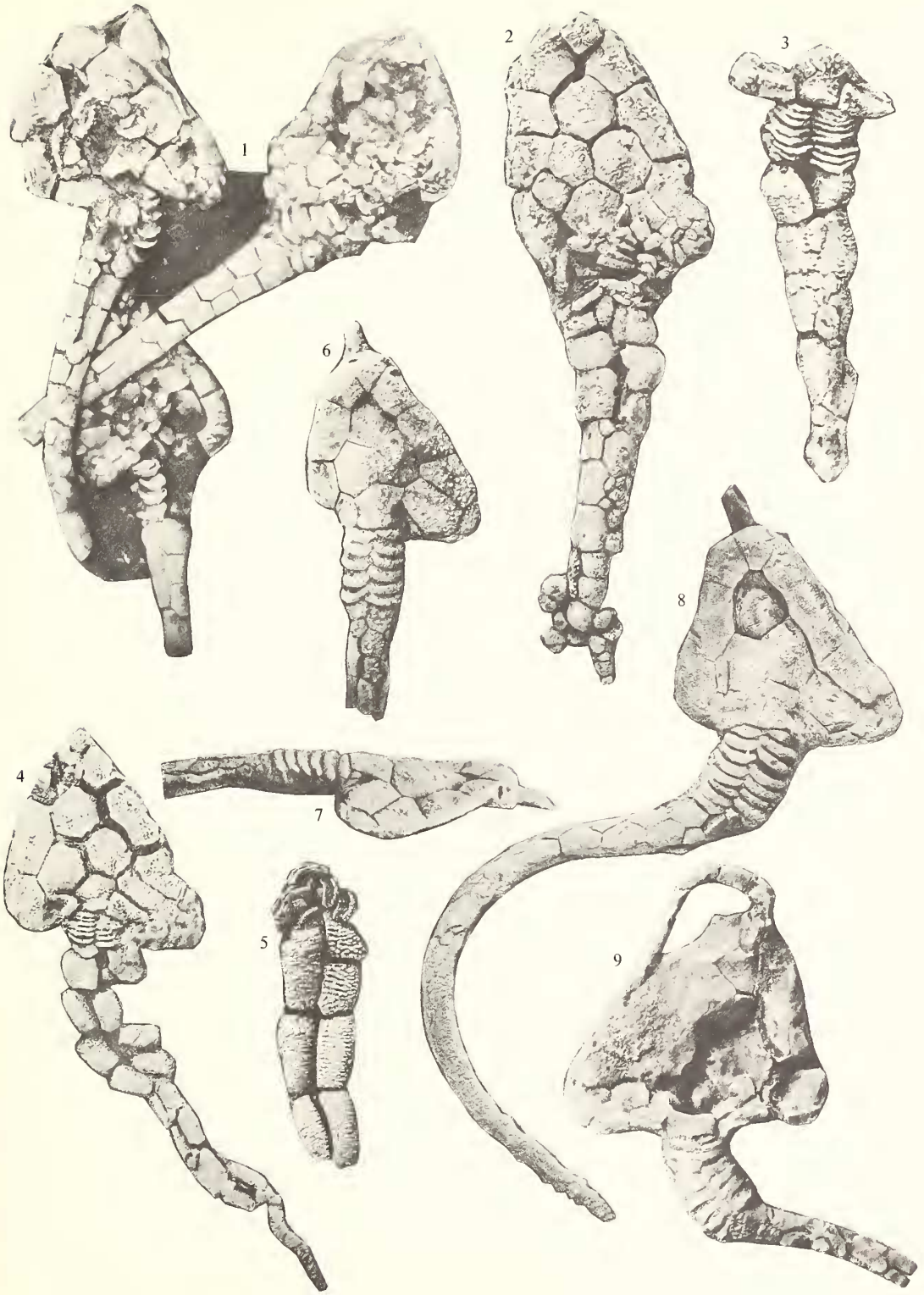
The proxistele and distal stele are differentiated and well developed in the earliest growth stages represented. The axial sutures on both sides of the distal stele are shaped like braces ({) lined end-to-end in an alternating pattern (Pl. 62, fig. 10). These arcuate sutures gradually become more linear during growth. The biserial structure of the distal stele is very much evident in the early growth stages; however, new plates were intercalated along the axial suture on the aboral side throughout ontogeny, resulting in a polyplated condition in the adults.

Remarks. The aboral thecal plates in *Iowacystis* can readily be homologized with those in *Scalenocystites* and *Belemnocystites* (text-fig. 8), but there are differences in the arrangement of the marginal plates. In *Iowacystis* (A), marginal M7 is typically separated from the aboral somatics by M6 and M8. In addition, the network of ridges and grooves along the marginal edges is more highly developed in *Iowacystis.*

EXPLANATION OF PLATE 63

Figs. 1–5. *Iowacystis sagittaria* Thomas and Ladd. 1, SUI 39444 (aboral face), SUI 39445 (oral face), and SUI 39446 (oral face), left, right, and lower respectively; Fort Atkinson Formation (bed no. 9 of Parker *et al.* 1959), Maquoketa Group, at Fort Atkinson, Iowa, ×1·6. 2, aboral face of SUI 39439; Elgin Member (bed no. 4 of Parker *et al.* 1959), Scales Formation, Maquoketa Group, Fort Atkinson, Iowa, ×2·5. 3, aboral face of SUI 39438; same locality as fig. 2, ×3. 4, aboral face of SUI 39441; Elgin Member (bed no. 4 of Parker *et al.* 1959), near Ossian, Iowa, ×2. 5, oral face of SUI 39447 showing pustules on distal stele; same locality as fig. 2, ×3·5.

Figs. 6–9. *Scalenocystites strimplei* Kolata. Sherwood Member, Dunleith Formation (Cummingsville Member of Weiss 1955, p. 1027), Galena Group, near Cannon Falls, Minnesota, ×3. 6–7, aboral face and lateral view of anal lobe of paratype SUI 37048. 8, aboral face of the holotype SUI 37017. 9, oral face of UI X-4895 showing nearly complete arm curved back against theca.



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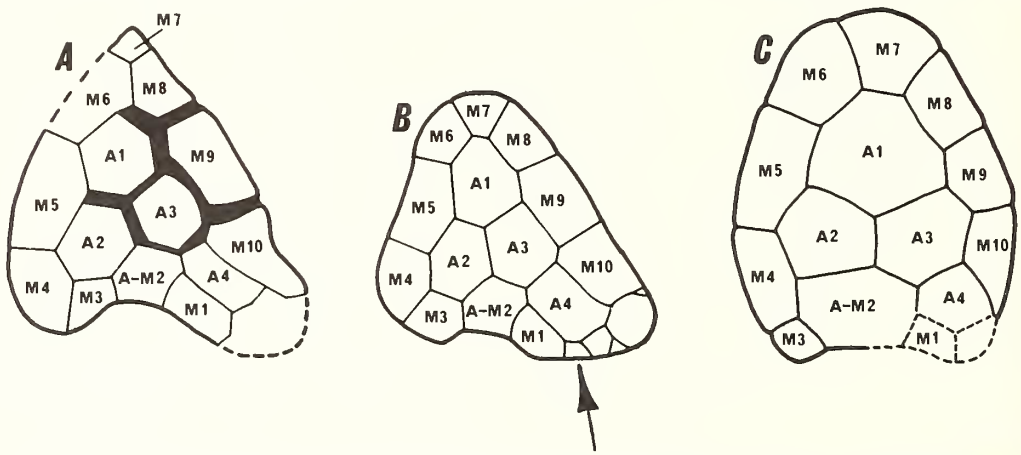
Iowacystis also possesses more adanal plates. The plates surrounding the base of the arm (adbrachials) on the oral face of the four known genera can confidently be homologized. The remaining oral face plates, however, vary in size, shape, and position so that homologies are not apparent. The structure of the arm and stele in *Iowacystis* is very similar to that of *Scalenocystites* and *Myeinocystites*.

Iowacystis appears to be most closely related to *Scalenocystites*. Both genera possess a triangular theca characterized by numerous plates on the oral face. The relations are particularly obvious when immature individuals of *Iowacystis* are compared with adult *Scalenocystites*. In the early stages of ontogeny, *Iowacystis* posesses an unusually large anal lobe, resulting in a scalene-triangle-shaped thecal outline that is very similar to that of *Scalenocystites*. If *Scalenocystites* is a Middle Ordovician ancestor of the Upper Ordovician genus *Iowacystis*, or is close to the



TEXT-FIG. 8. Homologous aboral plates in the three iowacystid genera. A, *Iowacystis sagittaria* Thomas and Ladd, 1926, SUI 39441. B, *Scalenocystites strimplei* Kolata, 1973, holotype SUI 37017; suspected modified adanal plate shown at arrow. C, *Belemnocystites wetherbyi* Miller and Gurley, 1894, holotype FMNH UC 6046; reconstruction of proximal plates based on topotype USNM 14201. Approx. ×2·5.

lineage that led to *Iowacystis*, as it would appear, then it is quite possible that the similarities between the two genera are due to recapitulatory effects. That is to say, the scalene shape with large anal lobe appears earlier in the descendant's (*Iowacystis*) ontogeny than in that of the ancestor (*Scalenocystites*). In addition, compared to the ontogeny of *Scalenocystites*, the scalene outline in *Iowacystis* appears at a larger thecal size.

The unusual cusps, nodes, arcuate ridges, and grooves along the edge of the marginals in *Iowacystis* are noteworthy. Thomas and Ladd (1926, p. 10) carefully described the structures and stated, 'The elaborate system of grooves and ridges on the marginals and their evident continuity from plate to plate along the periphery of the theca suggest that they may have had a part to play in the economy of the animal other than decoration'. Parsley and Caster (1965, p. 152) gave a detailed description of the structures and proposed a possible function, stating, 'It is possible that this network contained tissue of unusual thickness (i.e., for the external surface of

echinoderm) and may have functioned as a respiratory organ and a sensory system as well'. A similar although much less well-developed pattern of arcuate ridges occurs along the marginals in *Scalenocystites*. These ridges loop back and forth from one side of the theca to the other in a manner similar to the ridges of *Iowacystis*.

Genus SCALENOCYSTITES Kolata, 1973

Type species. Scalenocystites strimplei Kolata, 1973, p. 970.

Diagnosis. Scalene-triangle-shaped thecal outline with large anal lobe; somatic A1 in contact with marginal M7; numerous oral-face plates; base of arm and subthecal mouth typically enclosed by four adbrachial plates; distal stele consists of four plates at juncture with proxistele.

Scalenocystites strimplei Kolata, 1973

Plate 63, figs. 6–9; text-figs. 2, 3, 4, 8B, 9

Type specimens. The holotype (SUI 37017) and three paratypes (SUI 37018, 37047, and 37048) are in the repository, Department of Geology, University of Iowa, Iowa City, Iowa. Paratype UI X-4878 and topotype UI X-4895 are reposited in the type collection of the Department of Geology, University of Illinois, Urbana, Illinois.

Age. Champlainian Series (Middle Ordovician–Caradocian), Trentonian Stage.

Locality. The type specimens are from the argillaceous, buff-coloured calcisiltite of the upper part of the Sherwood Member, Dunleith Formation (Cummingsville Member of Weiss, 1955, p. 1027), Galena Group, at the Wagner Quarry on U.S. Highway 52, 8·8 km south of Cannon Falls, Goodhue County, Minnesota, W. SE. Sec. 8, 111N.–17W., Sogn Quadrangle.

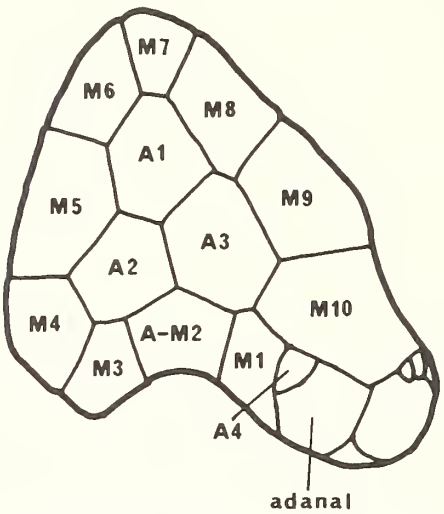
Diagnosis. Same characteristics as genus.

Description: Theca. The theca is depressed and generally biconvex in cross-section and is characterized by a large anal lobe. The thecal outline is in the form of a scalene triangle, and the thecal faces are differentiated.

The aboral face consists of thick plates that are uniform in size, shape, and position. Ten marginal plates (excluding marginal O-M2 and the anal plates) form a rigid frame to the theca. On some specimens an additional marginal plate occurs between M1 and the anal plates (text-fig. 8B); it appears to be modified adanal plate. An inner groove (visible on the inside edge of the marginals when the oral face is up) marks the edge of the body cavity and encircles the theca, as in *Iowacystis*. On the aboral face there is a reverse in curvature between the slightly concave marginals and the convex somatic plates. The distal edge of marginal M7 is turned up slightly.

Marginals M3 and M4 occupy the right (oral face up) proximal angle of the theca. Marginal M7 is at the distal tip, separating M6 and M8, and is in contact with somatic A1. A marginal flange extends out over the first proxistele tetramere. The marginal plates are marked by a faint arcuate ridge that curves around the thecal edges, looping from one marginal to another in a manner similar to the prominent ridge in *Iowacystis*. The ridge is especially well developed on the larger, presumably more mature, specimens (e.g. UI X-4878 and X-4895). Nodes, cusps, and secondary ridges are present on some of the larger specimens but are not as well developed as those in *Iowacystis*.

Typically four aboral somatic plates are present, including the distal A1, central A2 and A3, and a right proximal A4. Somatic A1 is heptagonal, and A2 and A3 are hexagonal. The A4 is generally heptagonal or octagonal and is the same size as the other somatics. In one specimen (UI X-4878) the A4 is poorly developed, and its position is occupied by an unusually large M10 and a large marginal plate of questionable homology that is located between the M1 and the adanals (text-fig. 9).



TEXT-FIG. 9. *Scalenocystites strimplei* Kolata, 1973, paratype UI X-4878, showing unusually large M10 and small A4. Approx. ×4·5.

The oral face consists of thirty-five to fifty relatively thin plates that apparently were loosely articulated. In most specimens the plates have disarticulated and collapsed on to the inside surface of the more rigid aboral face. In the specimens examined, the pattern of plates on the oral face is generally similar. The larger plates are fairly consistent in shape and position. Minor variations in pattern occur, particularly in or near the anal lobe where plates vary in number. The oral face plates are sutured to the marginals along the marginal lip.

The base of the arm and subthecal mouth are typically enclosed by four adbrachial plates. These plates are tilted distally in such a way that the brachial foramen is very close to the distal margin of the theca. The O1 and O2 plates are in positions similar to their places in other iowacystid genera, and the O3 plate is often compound. The adbrachials are tightly sutured to one another, as well as to marginals M6, M7, and M8. The O1 plate is sutured to M7 and M8, and possesses a prominent hydropore

EXPLANATION OF PLATE 64

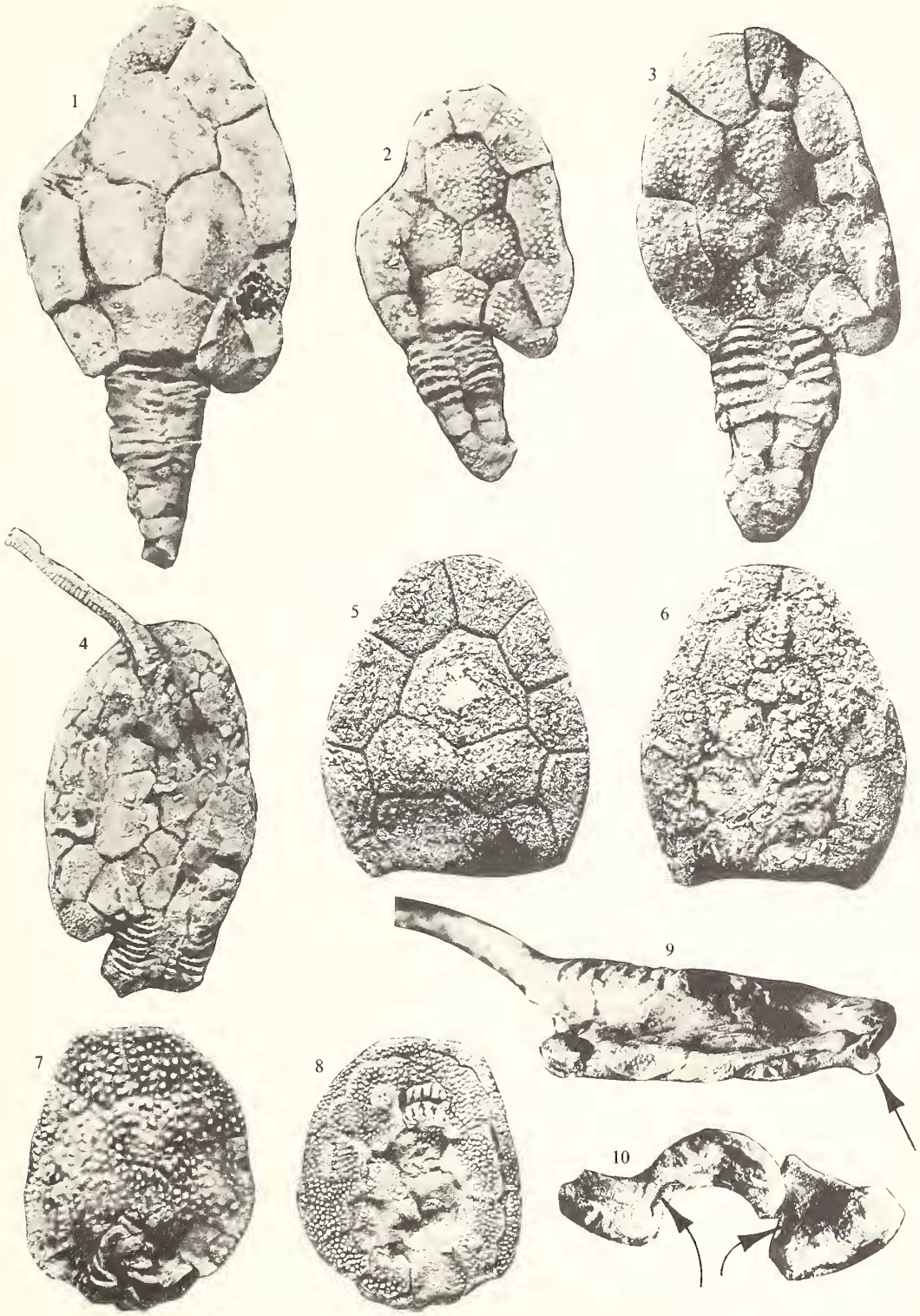
Figs. 1–4. *Myeinocystites crossmani* n. sp. 1–2, aboral faces of paratypes SUI 39452 and SUI 39453, respectively; Sherwood Member, Dunleith Formation, Galena Group, near Burr Oak, Iowa. 3, aboral face of holotype UI X-4879; Eagle Point Member, Dunleith Formation, near Rockton, Illinois. 4, oral face of paratype SUI 39451; same locality as figs. 1–2. All ×3.

Figs. 5–6. *Belemnocystites wetherbyi* Miller and Gurley. Curdsville Limestone near High Bridge, Kentucky, ×2·5. Aboral and oral faces of the holotype FMNH (UC) 6046.

Figs. 7–8. *Myeinocystites natus* Strimple. Bromide Formation, near Ardmore, Oklahoma, ×4. Aboral and oral thecal faces, respectively, of USNM (S) 5736.

Fig. 9. *Scalenocystites strimplei* Kolata. Sherwood Member, Dunleith Formation (Cummingsville Member of Weiss 1955, p. 1027), Galena Group, near Cannon Falls, Minnesota, ×3. Lateral view of right thecal edge (aboral face up) of UI X-4878 showing ridges, nodes, and cusps on marginals; hydropore tubercle at arrow.

Fig. 10. *Iowacystis sagittaria* Thomas and Ladd. Elgin Member (bed no. 4 of Parker *et al.* 1959), Scales Formation, Maquoketa Group, Fort Atkinson, Iowa, ×6·5. Interior view of adsteleal plates M1, A–M2, and M3 (left to right) of SUI 39438; grooves along the inner edge of M1 and M3 are shown by arrows.



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tubercle that is oriented at an oblique angle and projects out along the distal margin of the theca. Four to six pores pass to a small vestibule or depression on the inner surface of the O1 plate. The O1 and O2 plates are sutured to one another at the distal thecal tip beneath the arm. The remainder of the brachial foramen is enclosed by the compound O3 plate.

One or two plates occur along the proximal edge of A4 between M1 and the quarter-sphere anal plates. They are probably adanal plates that have become incorporated into the thecal margin. Although small adanals are present in some specimens along the margin between M10 and the quarter-spheres, they are seldom present between A4 and the quarter-spheres, as they are in *Iowacystis*.

Both faces of the theca are covered with pustules. Those on the aboral face are relatively large and widely spaced, whereas the pustules on the oral face are smaller and more densely packed. The stereomic microstructure is porous near the plate centres but becomes much more dense at the plate boundaries and in the pustules.

Arm. The arm emerges from the oral face at or near the distal margin of the theca. It is slender, nearly half again the length of the theca, and consists of a large biseries of brachial platelets that carry the ambulacral groove and a smaller biseries of erectile cover platelets (text-fig. 2). When viewed aborally, the brachial platelets can be seen to alternate in a chevron pattern with the vertices pointing towards the theca. The brachial platelets form the sides of the arm and imbricate along the distal edges. One cover platelet is matched to every brachial platelet on the adoral side along a slightly depressed line on each side of the ambulacral groove. When closed the cover platelets meet in a zigzag line to form a sharp medial crest along the adoral side.

Stele. The proxistele consists of five to seven telescopically imbricated tetramere rings, and the distal stele is composed of thick, elongate, polygonal plates. Throughout its length the stele is round in cross-section. The tetramere rings enclose a large lumen that tapers to the tip of the distal stele. The distal stele typically consists of four plates at the juncture with the proxistele. Within this zone the stele tapers abruptly to a long slender section. The distal stele plates are arranged in a biseries that is obscured somewhat by the presence of intercalary plates that distally increase in number. The entire distal stele is covered to the distal tip by numerous small pustules. Some plates near the distal end are thickened to form short blunt spines that impart a serrate outline to the stele.

Ontogeny. Eight specimens were examined that had thecal lengths ranging from 9 to 12 mm. The smaller, presumably immature, specimens possess a relatively large anal lobe and a poorly developed right proximal (oral face up) thecal lobe. Development appears to have led to a higher degree of bilateral symmetry. The thecal edges in the smaller specimens are sharp, whereas those in the larger are thickened slightly and possess ridges, nodes, and cusps similar to those of *Iowacystis*.

Remarks. Scalenocystites appears to be most closely related to *Iowacystis*. Both genera possess a triangular-shaped theca with numerous oral face plates, a marginal hydropore, and ridges, cusps, and nodes on the marginals. *Scalenocystites* differs, however, in its scalene-triangle-shaped theca, in number and arrangement of thecal

plates, and in its smaller size. The similarity of the plate pattern on the aboral face and the structure of the arm and stele suggest an affinity with *Belemnocystites* and *Myeinocystites*.

Genus BELEMNOCYSTITES Miller and Gurley, 1894

Type species. Belemnocystites wetherbyi Miller and Gurley, 1894, p. 9.

Diagnosis. Oval-shaped thecal outline; thecal edges sharp; marginals supposedly extend equally across both faces; arm and hydropore relatively far removed from thecal edge.

Belemnocystites wetherbyi Miller and Gurley, 1894

Plate 64, figs. 5–6; text-figs. 5, 8c, 10

1894 *Belemnocystites wetherbyi* Miller and Gurley, p. 9, pl. 1, figs. 4–6.
1968 *Belemnocystites wetherbyi* Miller and Gurley; Parsley *in* Caster, p. S623, fig. 395.
1972 *Belemnocystites wetherbyi* Miller and Gurley; Parsley, p. 342, pl. 1, figs. 1–8.

Material. The holotype (FMNH UC 6046) is in the Field Museum of Natural History, Chicago, Illinois, and a probable topotype (USNM 14201) is in the U.S. National Museum of Natural History, Washington, D.C. No other specimens are known.

Age. Champlainian Series (Middle Ordovician–Caradocian), Trentonian Stage.

Locality. The type specimens are from the Curdsville Limestone near High Bridge, Mercer County, Kentucky.

Diagnosis. Same characteristics as genus.

Description. The holotype (FMNH UC 6046) is a complete, partially silicified theca 19·0 mm long and 15·5 mm wide (Pl. 64, figs. 5–6). A small portion of the arm, with some seven or eight segments, is preserved on the oral face.

The thecal outline is ovate and the broader end proximal. The theca is depressed and biconvex in cross-section and appears to have suffered little preservational distortion. On the aboral face there is a reverse in curvature between the slightly concave marginals and the convex somatic plates. The thecal edges are sharp and lack ridges, cusps, and nodes. The arm is attached to the oral face towards the distal edge but not at the margin.

The plate pattern on the aboral face is like that in the other iowacystids (text-fig. 8c). Marginals M6 and M7 occupy the distal tip of the theca, and the suture between them lies on or close to the plane of symmetry. The right (oral face up) proximal thecal angle is formed by A3.

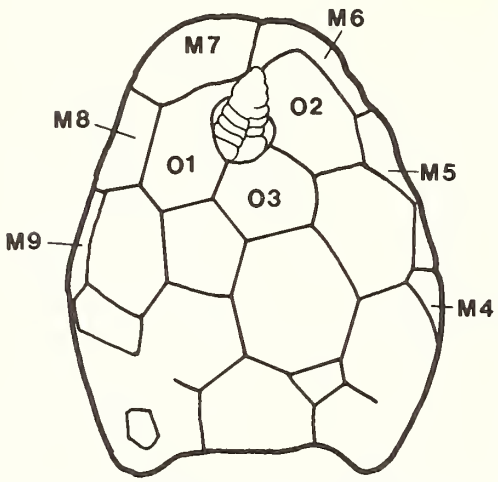
Four aboral somatic plates are enclosed within the marginal series. The distalmost somatic A1 is heptagonal in outline and is generally the largest of the four plates. Somatics A2 and A3, typically pentagonal and hexagonal, respectively, are centrally located and approximately equal in size. The relatively small A4 is in the right proximal thecal angle between A3 and the anal plates. Somatics A1, A2, and A3 are markedly convex.

The unusual adsteleal plates described by several authors (Wetherby 1881, p. 177, pl. 5, fig. 2, 2*a*; Miller and Gurley 1894, p. 9, pl. 1, figs. 4–6; marginals M1 and M′1

of Parsley 1972, p. 342, text-fig. 1C–E) cannot be substantiated in the holotype or in any other specimens now known. Comparison with the topotype supports the reconstruction of the proximal theca shown in text-fig. 8C.

The oral face is poorly preserved in the holotype and as a result the exact number and shapes of the plates are questionable. Most authors (Miller and Gurley 1894, p. 8, pl. 1, figs. 4–6; Parsley *in* Caster 1968, p. S623, fig. 395; Parsley 1972, p. 343, text-fig. 1C–D) describe the marginal plates as extending equally across both thecal faces, and note that five or six oral somatic plates appear in the centre of the oral face. Such an interpretation is based primarily on the apparent alignment of marginal sutures on both thecal faces.

The base of the arm and subthecal mouth are enclosed by two or three adbrachial plates. Unlike *Scalenocystites* and *Iowacystis*, however, the adbrachials are not distally angled in a way that brings the arm base close to the thecal margin. Adbrachial O1 has one, or possibly two, hydropore tubercles close to the arm and well removed from the thecal margin. Adanal plates are limited to one or two small elements along the thecal edge. The original pustulose surface ornament is preserved in a few areas on the oral face.



TEXT-FIG. 10. *Belemnocystites wetherbyi* Miller and Gurley, 1894. An interpretation of the oral face of the holotype (FMNH UC 6046). ×3.

The arm rests in a depression that extends between its base and the distal edge of the theca. The exact length of the arm is not known, but it was very likely as long as the theca. The general structure of the arm appears to be very similar to that of other iowacystid species. A large biseries of brachial platelets is covered by a smaller biseries of erectile cover platelets.

Neither of the two known thecae have any part of the stele attached. The stele is assumed to be similar to that of other iowacystid species.

The topotype is a complete theca, 17 mm long and 13 mm wide. Plate outlines are well preserved on the aboral face but have been obliterated by recrystallization on the oral face. Like the holotype, the topotype is partially silicified.

The plating arrangement in the topotype is like that in the holotype except that topotype marginals M9 and M10 are fused. A circular adsteleal foramen is formed in part by M1, A-M2, and M3; there are strong indications that the same condition existed in the holotype.

Remarks. Problems in interpreting the poorly preserved type material have led to differences of opinion between two of the authors of this paper. Kolata believes that plate boundaries, although obscure because of recrystallization, are visible along the edge of the oral face of the holotype and that they support the reconstruction shown in text-fig. 10. These plate boundaries are best seen (under binocular microscope)

when light is carefully reflected from the optically oriented crystals within the plates. Sutures corresponding to the reflected boundaries are preserved in some places. According to this interpretation, the pattern of the oral face plates in *Belemnocystites wetherbyi* is essentially the same as that in *Myeinocystites natus*. If correct, this would mean that *Myeinocystites* should be synonymized with *Belemnocystites*. Strimple disagrees with this interpretation and believes that the poor preservation precludes recognition of discrete plates and that stability of nomenclature requires retention of both genera until more definitive material is found.

Genus MYEINOCYSTITES Strimple, 1953

Type species. Myeinocystites natus Strimple, 1953, pp. 105–106; 1961, pp. 184–185.

Diagnosis. Oval-shaped theca; thecal edges sharp; thirteen to fifteen plates on oral face; marginal plates confined to narrow rim on oral thecal face; base of arm enclosed by three adbrachial plates; arm and hydropore relatively far removed from thecal edge.

Myeinocystites natus Strimple, 1953

Plate 64, figs. 7–8

1953 *Myeinocystites natus* Strimple, pp. 105–106, figs. 1–2.
1961 *Myeinocystites natus* Strimple; Strimple, pp. 184–185.
1972 *Myeinocystites natus* Strimple; Parsley, p. 344, pl. 1, figs. 9–14.
non 1975 *Myeinocystites natus* Strimple; Kolata, p. 15, pl. 1, figs. 8–10.

Material examined. The holotype is USNM (S) 4657 and a topotype is USNM (S) 5736 (Pl. 64, figs. 7–8).

Age. Champlainian Series (Middle Ordovician–Caradocian).

Localities. The type specimens are from the Bromide Formation in a bank of Spring Creek, Criner Hills, 11·2 km south-west of Ardmore, Oklahoma. Single specimen (FMNH PE 15647) is known from the Benbolt Formation, 2·4 km west of Washburn, Tennessee, on Highway 131, but it was not available during our investigation. The specimens assigned to *M. natus* by Kolata (1975, p. 15) from the Dunleith Formation of northern Illinois are herein reassigned to *M. crossmani* n. sp.

Diagnosis. A species of *Myeinocystites* characterized by a relatively small aboral, somatic A4 that is not in contact with the proxistele.

Description. The holotype (USNM S 4657) is a complete theca 16·5 mm long and 14·0 mm wide. Part of the arm and seven or eight proxistele tetrameres are intact. The thecal outline is ovate with the broader end proximal. The theca is depressed and was probably distorted during fossilization. As in *B. wetherbyi*, the aboral face is slightly concave along the sutures between the marginals and somatics. The thecal edges are tapered and lack ridges, cusps, and nodes.

Marginal and somatic plates on the aboral face can confidently be homologized with the other iowacystids. Except for the relatively small somatic A4, the aboral plates are similar to those of *B. wetherbyi* in size, shape, and arrangement. The marginal plates are bent abruptly at the thecal edges and are confined to a narrow rim on the oral face.

The oral face consists of thirteen to fifteen relatively thin plates that are disarticulated and fractured in some places. The plates have collapsed on to the inside surface of

the more rigid aboral plates. The oral face plates are sutured to the marginal plates along the marginal lip, as they are in *Scalenocystites* and *Iowacystis*.

The base of the arm is surrounded by three adbrachial plates homologous to those in *Scalenocystites* and *Iowacystis*. Adbrachial O1 possesses a prominent, cone-shaped hydropore tubercle. The O1 and O2 plates are sutured to each other between the base of the arm and the distal edge of the theca. The remainder of the brachial foramen is enclosed by the O3 plate.

The quarter-sphere anal plates lie along the proximal margin in the same relative position as those of the other iowacystids. Two or three small adanal plates appear on the oral face.

Both thecal faces and the proxistele are covered with pustulose ornament. Pustules on the aboral face are relatively large and widely spaced, whereas those on the oral face are smaller and more densely packed. The pustulose ornament is also quite pronounced in the topotype (Pl. 64, figs. 7–8).

A small part of the arm that has about ten segments is attached to the distal oral face. The arm is like arms of other iowacystids in that it consists of two matching but unequal biseries of plates. It rests in a slight depression between adbrachials O1 and O2.

About seven or eight telescopically imbricated proxistele tetrameres are intact. No part of the distal stele is preserved.

The topotype is a complete theca, 10·0 mm long and 8·5 mm wide, with part of the arm and proxistele intact. Plate patterns on the aboral and oral faces are like those in the holotype. The topotype differs in that on its aboral face the marginals occupy a relatively larger area than the somatics. Similar variation has been observed in the immature stages of *Iowacystis*. It is probably due to ontogenetic variation.

Parsley (1972, p. 344) assigned a specimen (FMNH PE 15647) to *M. natus* from the Benbolt Formation of Tennessee. The plating arrangement on the oral face of this specimen is quite similar to that of the topotype discussed above.

Myeinocystites crossmani n. sp.

Plate 64, figs. 1–4; text-fig. 11

1975 *Myeinocystites natus* Strimple; Kolata, p. 15, pl. 1, figs. 8–10.

Material. The holotype (UI X-4879) is in the type collection of the Department of Geology at the University of Illinois, Urbana, Illinois. One paratype (BMNH PK-70) is deposited in the Burpee Museum of Natural History, Rockford, Illinois. Three paratypes, SUI 39450, 39451, and 39452 are in the repository of the Department of Geology at the University of Iowa, Iowa City, Iowa.

Derivation of name. Specific appellation is for Glenn C. Crossman, who discovered some of the type material.

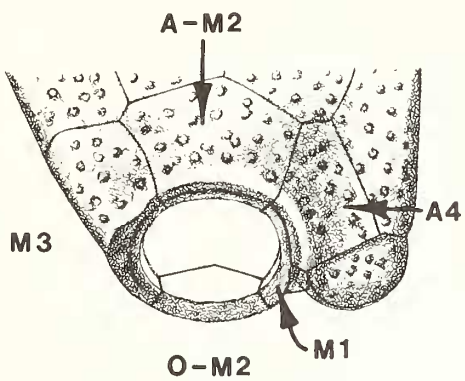
Age. Champlainian Series (Middle Ordovician–Caradocian), Trentonian Stage.

Locality. The holotype and one paratype (BMNH PK-70) are from the basal cherty dolomite of the Eagle Point Member, Dunleith Formation, Galena Group, in the Porter Brothers quarry 1·2 km south of Rockton, Winnebago County, Illinois, NW. SE. NE. Sec. 35, 46N.–1E., South Beloit 7·5-minute Quadrangle. The remaining paratypes are from the cherty, partly calcarenitic limestone at the top of the Sherwood Member, Dunleith Formation, Galena Group, in a quarry located approximately 0·7 km north-west of Burr Oak, Winneshiek County, Iowa, SW. SE. Sec. 14, 100N.–9W., Decorah 15-minute Quadrangle.

Diagnosis. A species of *Myeinocystites* characterized by a relatively large aboral somatic A4 that is in contact with the proxistele.

Description. Thecal outline is a relatively elongate, asymmetric oval. Right proximal thecal lobe (oral face up) not well developed; left margin nearly continuous with stele. The theca is depressed and biconvex in cross-section.

The aboral face consists of regular marginal and somatic plates that are homologous to other iowacystids. The marginal plates occupy a relatively large area on the aboral face, but they are confined to a narrow peripheral band on the oral face. Adsteleal M1 is very small and in most specimens is usually concealed between somatic A4 and the proxistele (text-fig. 11). Somatic A4 is in a marginal position and appears to have functioned as an adsteleal plate in conjunction with M1.



TEXT-FIG. 11. *Myeinocystites crossmani* n. sp., proximal view of theca showing the adsteleal plates. ×4·5.

The oral thecal face is not well preserved in the specimens studied here. From all indications it consists of thin plates arranged in a pattern similar to that of *M. natus*. The base of the arm and the subthecal mouth are surrounded by three adbrachials (O1, O2, and O3). The hydropore consists of four or five small pores. The arm rests in a shallow depression along the O1–O2 suture.

The two quarter-sphere plates of the anus are located along the margin of the right proximal lobe between the M1 and M10. No additional adanal plates were observed.

Both thecal faces are covered with pustules. Pustules on the aboral face are relatively large and widely spaced, whereas those on the oral face are small and densely spaced. Pustules also occur on the distal stele.

Arm. The arm is slender, and its length was probably equivalent to that of the theca (Pl. 64, fig. 4). It consists of a large biseries of brachial platelets covered on the oral side by a smaller biseries of erectile cover platelets that meet on the median along a zigzag line.

Stele. Only the proxistele and a small part of the distal stele are preserved in the specimens examined here. The proxistele consists of six to ten telescopically imbricated tetramere rings with plane of symmetry sutures forming an irregular zigzag line. The extensiplane sutures are closely appressed and lack the zigzag pattern.

The distal stele consists of four plates at the juncture with the proxistele and has sutures in the plane of symmetry and extensiplane. In cross-section four or five polygonal plates surround a large, round lumen that extends distally.

Remarks. The holotype of *M. crossmani* n. sp. was previously assigned by Kolata (1975, p. 15) to *M. natus* Strimple. It is now apparent, however, that *M. crossmani* differs from *M. natus* in possessing a relatively large A4 somatic plate that is in contact with the proxistele.

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